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The effect of temperature on herbivory by the omnivorous ectotherm snail *Lymnaea stagnalis*

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Abstract Rising temperatures likely affect the trophic interactions in temperate regions as global warming progresses. An open question is how a temperature rise may affect consumer pressure and plant abundance in shallow aquatic ecosystems, where most consumers are omnivorous. Interestingly, herbivory (plant-eating) is more prevalent toward low latitudes in ectotherms such as fish and aquatic invertebrates, and this may be temperature driven. We used pond snails (*Lymnaea stagnalis* L.) as a model aquatic ectotherm species and tested their consumption of both animal prey (*Gammarus pulex* L.) and plant material (*Potamogeton lucens* L.) at three different temperatures (15, 20, and 25°C). Higher temperatures led to higher consumption rates by the omnivore on both plant food and animal prey when fed separately. When the food was offered simultaneously, the pond snails consistently preferred animal prey over plant material at all tested temperatures. However, the omnivore did consume plant material even though they had enough animal prey available to them. Based on our experiments, we conclude that with increasing temperatures, *L. stagnalis* will only increase their consumption rates but not change food preference. Further studies are needed to test the generality of our findings across aquatic species to predict the effect of warming on aquatic plant consumption.

Keywords Aquatic · Diet selection · *Lymnaea stagnalis* · Omnivore · Temperature · Trophic interaction

Introduction

Average water temperatures are increasing in many temperate lakes as a consequence of climate change (Mooij et al., 2008; Adrian et al., 2009). Biological responses to this temperature rise have already been observed: mean fish size decreases in temperate freshwater systems (Jeppesen et al., 2010; Meerhoff et al., 2012; Edeline et al., 2013), water bird migration is changing (Van Eerden et al., 2005; Van der Jeugd et al., 2009), and fish communities may be changing toward increasing abundance of fish with wide temperature tolerances (Jeppesen et al., 2012; Meerhoff et al., 2012) as well as fish becoming more

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omnivorous, e.g., including more plants in their diets (Jeppesen et al., 2010). An open question is how these changes may affect consumer pressure and plant abundance in shallow aquatic ecosystems. Whereas the temperature rise may generally enhance the growth rates of macrophytes and stimulate plant abundance (Rooney & Kalff, 2000; Feuchtmayr et al., 2009), increased consumption on plants may offset this benefit for the plants (O'Connor, 2009). Trophic downgrading, i.e., the shift toward more macrophyte consumption in food webs, can have a very strong impact on the vegetation, the organisms depending on it, and ultimately on ecosystem functions when temperatures increase (Estes et al., 2011; Strickland et al., 2013).

In aquatic systems, most animals consuming vascular plants are omnivorous, including both plant and animal material in their diet (González-Bergonzoni et al., 2012; Gross & Bakker, 2012; Wood et al., 2012). The prevalence of herbivory (plant-eating) varies with latitude: in fish communities, the level of herbivory strongly increases toward the equator (Floeter et al., 2005; Moss, 2010). This pattern is consistent with increased plant consumption at lower latitudes by invertebrates as well (Pennings et al., 2009; Schemske et al., 2009; González-Bergonzoni et al., 2012). However, it is debated which factors drive this pattern (González-Bergonzoni et al., 2012; Ho & Pennings, 2013). Ambient temperature, the evolutionary time to adapt to plant consumption, and food availability have been evoked as important explanatory factors (González-Bergonzoni et al., 2012). At higher temperatures ectotherm animals, such as fish, can better digest plant material (Clements et al., 2009). Indeed, plant consumption by fish shows a strong positive correlation with ambient temperature (Behrens & Lafferty, 2007, 2012), and above a threshold of 16°C plant consumption is found to be more common in freshwater fish (Prejs, 1984; Lake et al., 2002). Alternatively, more rapid evolution and shorter generation times (due to warmer temperatures) and absence of strong seasonal temperature fluctuations have contributed to the radiation of tropical species (Allen & Gillooly, 2006; Mittelbach et al., 2007) and may have allowed adaptation to plants as a food source. Another possibility is that there is simply less animal food available at low latitudes, resulting in increased plant consumption (Meerhoff et al., 2012). Therefore, it remains unclear whether temperature, evolutionary constraints on plant consumption, or food availability are driving the latitudinal gradient in plant consumption by fish. If temperature is an important driver of plant consumption, then this has important implications for the impact of a temperature rise on plant consumption in temperate regions. Therefore, experiments that test the effect of temperature on plant consumption are urgently needed.

In this study, we test whether and how different temperatures affect the consumption rates and diet selection of aquatic omnivorous ectotherms. Based on the literature, we hypothesize that the omnivore will select more plant relative to animal food at higher temperatures (Behrens & Lafferty, 2007, 2012). We chose the generalist omnivore *Lymnaea stagnalis* L. as a model aquatic omnivore species and conducted no-choice and choice feeding trials with plants (*Potamogeton lucens* L.) and animal prey (*Gammarus pulex* L.) at different temperatures.

Materials and methods

Model system

We chose *L. stagnalis* for our experiment, an omnivorous molluscan species that has often been used in feeding trials (Elger & Barrat-Segretain, 2002, 2004), and which is reported to feed on a variety of benthic and periphytic algae (Brönmark, 1989), vascular plants (Gaevskaia, 1969; Elger et al., 2004), as well as carrion, such as dead crayfish, insects, frog tadpoles, fish, and even snails (Bovbjerg, 1968). In the field, molluscs can have a large impact on macrophyte abundance (Lodge, 1991; Newman, 1991). *P. lucens* is one of the most preferred submerged macrophytes by *L. stagnalis* (Elger et al., 2004) and also a common macrophyte in the Netherlands. The crustacean *G. pulex* is one of the most important invertebrate species in temperate streams, which is widely distributed throughout Europe (Holdich & Pöckl 2007), and can reach a density of 10,000 m^{-2} and has a continued mortality throughout the year (Welton, 1979). *G. pulex* feeds on a variety of debris, such as oak and elm leaves (Sutcliffe et al., 1981). Ditches with oak trees along the banks are common in the

Netherlands, and there are also plenty of macrophytes and *L. stagnalis* in many of these ditches. The snails live in these ditches together with *G. pulex* which is present at a high density. The snails may intentionally or unintentionally incorporate some dead *G. pulex* in their diet. Considering their abundance and sympatry, we chose these three species as a snail-animal prey-plant model system to study the effect of changing temperatures on omnivorous diet choice.

Experimental subjects preparation

P. lucens shoots were sampled in a ditch close to Wageningen, the Netherlands (51.97°N, 5.62°E) and then acclimated at 20°C in the laboratory to prevent the decay of plant tissues during the one week storage period preceding the feeding trial. The *G. pulex* were collected in another small ditch close to Wageningen. *G. pulex* were sieved and pipetted into a groundwater-filled bucket (15L with aeration) with some degraded plant material from the same ditch to keep them alive. 131 *L. stagnalis* were collected from the ponds at the NIOO-KNAW, Wageningen, the Netherlands (51.99°N, 5.68°E) in June 2015. Snails were evenly divided into 3 plastic buckets (26 × 38 × 26.5 cm), each filled with 15 L of groundwater, and then put in temperature-controlled (15, 20, and 25°C) aquaria (50 × 185 × 50 cm) with a 16:8 day: night cycle to acclimatize 10 days before the feeding trials. The snails were fed butterhead lettuce for 5 days per week. Fish food pellets (Velda, Gold Sticks Basic Food) were supplied once a week to provide other nutrients, and half a piece of chalkboard chalk was supplied to provide calcium as the concentration of calcium in the ground water (36 mg L^{-1}) may be low for the calciphile species *L. stagnalis* (Van der Borght & Van Puymbroeck, 1966; Dalesman & Lukowiak, 2010). The water used to culture the snails was fully replaced once, and halfway through the culturing period several indicators of water quality were checked with a multi-meter (Multi 350i/SET, Germany). Average pH was 7.9 ± 0.2 (mean ± SD, $n = 3$) and average conductivity was 307 ± 25.3 µS/cm (mean ± SD, $n = 3$). Snails used in the trials had an average shell length of 27.1 ± 2.2 mm, wet weight with shell of 1.80 ± 0.44 g, and dry weight without shell of 0.12 ± 0.03 g (mean ± SD, $n = 108$).

Feeding trials

The feeding trials followed standard protocols developed for snails (Elger & Barrat-Segretain, 2002, 2004). Both no-choice (only one type of food) and choice (both types of food) trials were performed at 3 different temperatures. Each treatment (9 treatments in total) had 12 replicates, and in total 108 snails were used. The test temperatures 15, 20, and 25°C were chosen because the optimal temperature for the growth and reproduction of *L. stagnalis* is around 20°C and the snail will not feel stress at both 15°C and 25°C (Van der Schalie & Berry, 1973). Fresh undamaged *P. lucens* leaves with their midrib removed were offered to the snails as snails prefer the soft parts of the leaves over the midrib. Sub-adults and adults of *G. pulex* were killed in water of 45°C before being offered to the snails as snails cannot catch the living *G. pulex*; the *G. pulex* would not structurally degrade when killed at this temperature, as was shown from pilot trials. Pretrial pilots showed that no measurable plant growth nor animal prey weight loss occurred when these were left in water for 24 h at different temperatures, apart for the plant material at 25°C (Online resource 1). At this temperature, the plants lost on average almost 2% of weight, which was just significant (Online resource 1). Since this was such a low amount of weight loss, we decided to not further correct for it. Further pilot trials demonstrated that a snail consumed at maximum 0.15 g (wet weight) food in 24-h feeding. So both plant material and animal prey were weighed to approximately 0.18 g (wet weight) per portion to allow the snails ad libitum access to food during the feeding trials. For the no-choice trial, the amount of food was 0.18 g (wet weight) in each cup, but for the choice trial this was double the amount, about 0.36 g (wet weight) in each cup, because the snails needed ad libitum food for each food type. The mean number of *G. pulex* individuals offered in each cup was 9.2 ± 2.2 (mean ± SD, $n = 72$) throughout the entire experiment, and pretrial pilots showed that there was no relationship between consumption of animal prey and the number of animal prey individuals offered, as long as there were enough individuals offered to allow ad libitum feeding. Each snail was fed individually in a plastic cup (top diameter 9 cm, and height 11.5 cm) filled with 375 ml groundwater, which was acclimated to the experimental temperature (Online Resource 2).

The cups were covered with mesh to prevent the snails from escaping. Floating polystyrene foam platforms were used to hold the cups on top of the water in the aquarium. Less than one hour was spent in both putting the snails in the cups before the feeding trials and taking the snails out of the cups after the feeding trials; all the feeding trials were performed simultaneously. All snails were starved for 48 h before the start of the trials, and the feeding lasted for 24 h. After the feeding, left-over food was dried in an oven at 60°C for at least 48 h. All snails were first frozen to death at −20°C, the soft body of the snail was separated from its shell, and then the whole snail was dried in an oven at 60°C for at least 48 h. We measured carbon (C), nitrogen (N), and phosphorus (P) contents of random samples of *P. lucens*, *G. pulex*, and *L. stagnalis* bodies, $n = 3$ for each species. Dried samples were ground into fine powders. C and N were determined by an auto elemental analyzer (FLASH 2000, Thermo Scientific, Waltham, MA, USA). P was determined by first incinerating, digesting, and analyzing in an Auto Analyzer (QuAAtro method, Seal Analytical, Fareham, UK) (Grutters et al., 2015).

Data analysis

We followed the procedures of Elger & Barrat-Segretain (2002) to calculate the snail consumption rates of plant and animal prey. Extra *G. pulex* and *P. lucens* leaves were used to establish dry weight–wet weight regression lines, from which the initial dry weight of the food was back-calculated. The regression line for *G. pulex* was $y = 0.2005*x$ ($r^2 = 0.99$, $P < 0.001$, $n = 14$), with y giving dry weight in mg, and x being wet weight in mg. For *P. lucens* the regression line was $y = 0.2061*x$ ($r^2 = 0.98$, $P < 0.001$, $n = 30$), with y giving dry weight in mg, and x being wet weight in mg. Consumption rate was described as milligram dry weight of food and per gram dry weight of snail (without shell) consumed per day (Elger & Barrat-Segretain, 2002). The amount of food consumed was calculated by subtracting the dry weight of the left-over food from the calculated initial dry weight of food offered. One-way ANOVA was used to test the mean difference in consumption rate among temperature treatments, and the difference in nutrient concentration and stoichiometry between the food items and the consumer. Two-way ANOVA was used to test the interaction between temperature and the presence/absence of an alternative food source (choice and no-choice trials). Plant consumption rates and animal prey consumption rates were tested separately. Pearson correlation was used to test the relationship between plant material consumption and animal prey consumption in the choice trial. There were 4 negative values of 108 feeding trials, the negative values were most likely due to slight differences in the wet-dry weight ratio calculated from the calibration line, and we kept these values in the statistics. We used the ratio of the plant: animal consumption rate at each temperature to test the diet selection by the snails. To test for differences in plant consumption rate in the no-choice trials at different temperatures using a one-way ANOVA, we transformed the data by adding a value of $\log_{10}$ to make the variance homogeneous, which was confirmed using a Levene's test. Data were tested for normality using a Kolmogorov–Smirnov test. All tests were performed in SPSS 22.0 (IBM, 2013).

Results

The food items differed significantly in nutrient concentrations and most nutrient ratios from each other, and in several of these traits from the body composition of the consumer (Table 1). The plant leaves had an almost three times higher C:N and C:P ratio compared to both the animal prey and the snail body composition, the latter not being significantly different from each other. This was mainly driven by lower N and P concentrations in the plant material (Table 1). During the feeding trials, we observed the snails eating, they were enthusiastically feeding, they scraped the leaves, wrapped the whole *G. pulex* by their soft bodies. Pieces of animal prey bodies or scraps of plant leaves were found in almost all the cups after the feeding trials. During the feeding trial, the snails consumed large parts of the animal prey but less plant material. In the no-choice feeding trials, the wet weight of the consumed plants decreased from 0.19 ± 0.01 g to 0.15 ± 0.03 g (mean ± SD, $n = 35$), and for the animal prey from 0.18 ± 0.01 g to 0.08 ± 0.04 g (mean ± SD, $n = 36$), or in number from 8.2 ± 2.3 to 2.2 ± 1.7 (mean ± SD, $n = 36$) of undamaged *G. pulex* individuals left at the end of the feeding trials. In the choice trials, the wet weight of the consumed plants decreased from 0.19 ± 0.01 g to

Table 1 Nutrient content and stoichiometry in the food items (plant leaves and animal prey) and the consumer

	Plant leaves (*P. lucens*)	Animal prey (*G. pulex*)	Omnivore (*L. stagnalis*)	*F*	*P*
C (mg g^{-1})	397 ± 2.5[a]	347 ± 18[b]	430 ± 6.6[c]	290.1	<0.001
N (mg g^{-1})	30.8 ± 0.62[a]	77.8 ± 5.8[b]	100 ± 3.8[c]	236.6	<0.001
P (mg g^{-1})	3.17 ± 0.33[a]	8.53 ± 1.3[b]	7.59 ± 0.59[b]	34.10	0.001
C:N (g g^{-1})	12.9 ± 0.33[a]	4.48 ± 0.32[b]	4.29 ± 0.17[b]	928.6	<0.001
C:P (g g^{-1})	126 ± 13[a]	41.4 ± 6.2[b]	56.8 ± 3.8[b]	87.17	<0.001
N:P (g g^{-1})	9.76 ± 1.1[a]	9.23 ± 1.3[a]	13.3 ± 0.89[b]	11.93	0.008
Dry matter content (g g^{-1})	0.21 ± 0.02	0.20 ± 0.02	–	0.0002	0.476

Values are mean ± standard deviation (SD). Different superscript letters in the same row indicate a significant difference between the items (one-way ANOVA). For all the nutrient measurements $n = 3$. Dry matter content for plant leaves $n = 30$, for animal prey $n = 14$

0.18 ± 0.02 g (mean ± SD, $n = 36$), and for the animal prey from 0.18 ± 0.01 g to 0.08 ± 0.04 g (mean ± SD, $n = 36$), or undamaged individual in number from 10.1 ± 1.7 to 2.1 ± 1.8 (mean ± SD, $n = 36$). Snail consumption rates significantly increased as temperature increased in the no-choice feeding trials, both when the snails were fed with only plants ($F_{2,32} = 3.37$, $P < 0.05$) and only animal material ($F_{2,33} = 12.69$, $P < 0.001$) (Fig. 1a, b). Similarly, snail consumption rates increased with temperature when both food types were offered simultaneously in the choice feeding trials ($F_{2,33} = 6.06$, $P < 0.01$) (Fig. 1c). However the diet selection by the snails, expressed as the plant: animal consumption ratio, was not different among the temperature treatments ($F_{2,33} = 0.649$, $P = 0.53$) (Fig. 1d).

In the presence of animal prey, plant consumption rates were consistently lower compared to when plants were the only food type, and this was true at all tested temperatures (two-way ANOVA: effect of temperature, $F_{2,65} = 2.42$, $P = 0.10$; effect of choice/no-choice test, $F_{2,65} = 23.53$, $P < 0.001$; interaction, $F_{2,65} = 0.31$, $P = 0.97$). In the choice feeding trial, there was no difference in plant consumption between different temperature treatments ($F_{2,33} = 1.012$, $P = 0.38$) (Fig. 1c). The snails consumed equal amounts of animal prey both in the absence and presence of plants as alternative food source, independent of temperature (two-way ANOVA: effect of temperature, $F_{2,66} = 20.88$, $P < 0.001$; effect of choice/no-choice, $F_{2,66} = 0.17$, $P = 0.68$; interaction, $F_{2,66} = 2.27$, $P = 0.11$). Animal prey consumption rates significantly increased with increasing temperature in the choice trials ($F_{2,33} = 9.89$, $P < 0.001$). There was a significant positive correlation between the consumption of animal prey and plant material in the choice trial across all temperature treatments ($r = 0.43$, $P < 0.01$, $n = 36$) (Fig. 2).

Discussion

As temperature increased, both plant material and animal prey consumption increased in our study. Generally, within the tolerable temperature range, the metabolic rates of ectotherms increase exponentially with rising temperature and the consumption rates also increase (Gillooly et al., 2001). Previous studies have shown that metabolic rates increase faster than consumption rates in many ectotherms with a temperature rise (Kingsolver & Woods, 1997) which may lead to mismatch between consumption and digestion in ectotherms (Lemoine & Burkepile, 2012). One potential strategy to reduce the mismatch is to consume a diet with more carbohydrates which can be easily utilized for energy (Lee et al., 2015). This would imply selection for a more carbon-based diet with increasing temperatures and, hence, more plants and less meat for omnivorous ectotherms (Boersma et al., 2016).

Indeed, several studies support this hypothesis. Caterpillars increased their preference for

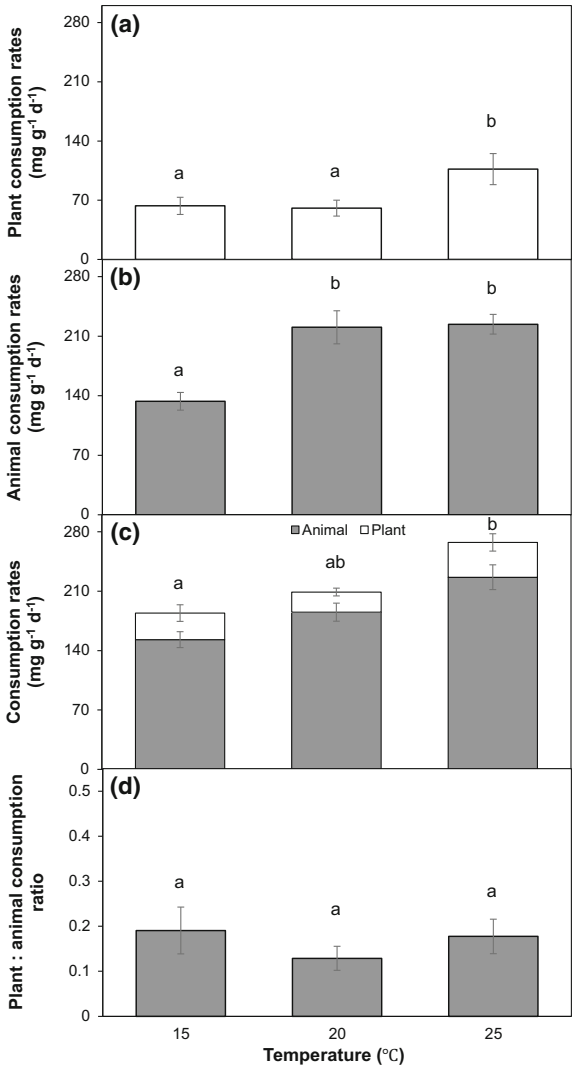

Fig. 1 Food consumption rates and diet selection. **a** Plant material consumption rates in the no-choice trial, **b** animal prey consumption rates in the no-choice trial, **c** both plant material and animal prey consumption rates in the choice trial, and **d** plant consumption: animal consumption ratio in the choice trial. *Different letters* indicate a significant difference between the two bars. *Error bars* indicate ± standard error (SE)

carbohydrates at higher temperatures (Lee et al., 2015), whereas omnivorous fish consume proportionally more plant material with increasing temperatures (Prejs, 1984; Behrens & Lafferty, 2007, 2012; González-Bergonzoni et al., 2015). Similarly, the herbivorous amphipod *Ampithoe longimana* Smith, 1873, collected in a cold-temperate environment, consumed

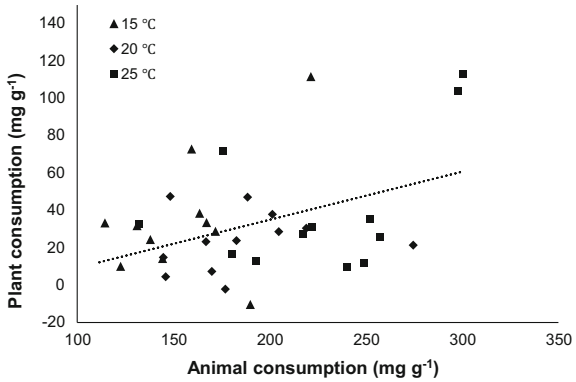

Fig. 2 Correlation between plant material consumption and animal prey consumption in the choice trial at all temperatures (Pearson correlation: $r = 0.424$, $P = 0.01$, $n = 36$). Consumption described as milligram food (dry weight) consumed by per gram snail (dry weight without shell)

more low organic and protein content seaweeds at higher temperatures (Sotka & Giddens, 2009). However, our results are in line with studies showing that a temperature rise does not alter food preference in ectotherms. For example, increased temperature did not alter the protein: carbohydrate consumption ratio by locusts (Miller et al., 2009; Clissold et al., 2013), and beetles consumed plants with higher, not lower, N content at higher temperatures (Lemoine et al., 2013). In line with these studies, we reject our hypothesis and conclude that in our study snails did not change their diet with increasing temperature.

The snails in our experiment consistently preferred animal prey over plants as food, regardless of temperature. The preference for animal prey could be explained by its stoichiometry with C:N and C:P ratios being much more similar to the body composition of the consumer than the offered plant material (Table 1). This was particularly due to the increased concentrations of N and P, whereas the C concentration was somewhat lower in the animal prey compared to the plant material, but the difference was not as large as in N or P. Consumers are predicted to preferentially eat food with a composition similar to their own bodies (Elser et al., 2000). A similar result was found in an experiment with fish where rudd and grass carp consistently preferred animal prey over plant food, both in short-term feeding trials at 18°C and in 10-week pond experiments with water temperatures varying from 16 to 24°C (Dorenbosch & Bakker, 2011, 2012).

Even though the omnivores showed a consistent strong preference for animal prey, they did consume plant material in the choice trial at all temperatures where both food types were presented ad libitum. Also, we found a significant correlation between animal prey consumption and plant material consumption when both food types were offered to the omnivorous consumer (Fig. 2). Most generalist consumers have a strategy involving feeding on mixed food to obtain a balanced nutrition intake (Behmer, 2009; Raubenheimer, 2011; Lihoreau et al., 2015). The snails in our experiment may have been balancing their nutrient intake by mixing animal prey with plant food.

There are some limitations to our study. We tested consumption rates and diet selection at three temperatures (15–25°C) which may be a relatively narrow range of temperatures compared to temperatures naturally experienced by aquatic snails. However, our chosen testing temperatures lie well within the range of those of other experimental studies revealing a diet switch from animal prey to plant food in aquatic ectotherms, for instance a marine fish tested at 12–27°C (Behrens & Lafferty, 2007) and copepods tested at 10–24°C (Boersma et al., 2016). In both studies, the observed diet switch was also visible within the 15–25°C temperature range. Therefore, the limitations of our experimental design do not explain the lack of diet switch by the snails. Possibly, not all ectotherms are capable of adjusting their diet with changing temperatures.

The study of the effects of rising temperature on trophic interactions becomes more urgent as global warming progresses. An increasing strength of plant–herbivore interactions has been found to coincide with rising temperatures (Barton et al., 2009; O'Connor, 2009; Shurin et al., 2012). Compared to the amount of studies currently investigating the effects of global warming on trophic interactions, there seems to be only relatively few studies investigating the role of omnivores in this situation (e.g., Boersma et al. (2016)). Our study indicates with increasing temperatures more plant consumption is expected by ectotherm omnivores due to increased consumption rates, not increased plant preference. However, to further generalize from our snail experiments to patterns of plant consumption by ectotherm omnivores in response to global warming, more experimental studies are needed, especially as the ones available to yield contrasting results.

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